CHAPTER 3

SALINITY, HALOPHYTES AND SALT AFFECTED NATURAL ECOSYSTEMS

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Abstract

A high diversity of halophytes has evolved in predominantly arid regions. The mechanisms of salt resistance are manifold. Classification of halophyte types can be done by using various parameters. Ion ratios play an important role in adaptation of halophytes. Succulence is a special feature of halophytes, enhanced by salts in stem- as well as in leaf-succulents. Recretion of salts by salt-glands or bladders is another mechanism to cope with salinity. Natural saline ecosystems are occurring worldwide along coasts, but at inland sites are created predominantly in arid regions.

3.1 Introduction

Potential evaporation in arid regions is higher than precipitation. Rainwater contains ions and run-off water is leaching rocks and soils. This leads inevitably to the accumulation of salts in soils, especially in the lower areas around the erosion basins. With the use of irrigation water the processes are the same but are much faster.

Erosion basins of the arid regions are thus saline and constitute the proper habitat for halophytic vegetation. This is characteristic of most of the arid endorrheic basins. Soils of irrigated agricultural fields of those regions exhibit a rather fast accumulation of salts.

Effects of salinity on the natural vegetation types are on various levels. Some 5% of the European flora are halophytic, whereas in the Iranian flora they reach some 7%. Such plants constitute the various halophytic vegetation types.

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Various types of salinity are known (chloride-, sulphate-, carbonate-, magnesium-, and boron-), depending on soil properties (Chapter 2), climatic conditions and ecosystem processes. The presence of excessive ions in such ecosystems dominates over many other environmental factors, and leads to an overall similar physiognomy of saline vegetation types, to a great extent irrespective of climate.

3.2 Mechanisms of salt tolerance in halophytes

3.2.1 TOLERANCE AND RESISTANCE

Plants are subjected to a variety of ecological factors, varying with space and time. It is generally accepted that tolerance to a specific ecological factor such as drought, frost, heat, salinity etc. is the more specific term to describe a distinct adaptation of a plant species in coping with the relevant stress-factor, whereas resistance is the overall general term (Waisel, 1972; Levitt, 1980). Salt resistance has different components. At the whole plant level it may be the process of salt regulation, but at the cellular level it may be the salt tolerance of the cytoplasm (Popp, 1985).

Plants growing naturally on saline stands have evolved various mechanisms to cope with salinity. Table 1 gives examples of control mechanisms in plants for maintaining a rather constant level of sodium concentration in the living plant tissues. This is regarded one of the major factors of adaptation in halophytes in contrast to that of non-halophytes ("glycophytes") besides of osmotic adaptation (see below).

TABLE 1. Control mechanisms of halophytes to strive on saline sites (Breckle, 1990)

A Avoidance		
	a	growth only during favourable seasons (time niche)
	b	growth only on favourable sites (site niche)
	c	limitation of root growth and absorption activity to distinct soil horizons (site niche)
B Evasion and adaptation processes		
	a	selectivity against Na and Cl
	b	leaching of salt from shoots
	c	diversion of salt out of assimilating tissues
	d	compartmentation of salt within plant, within tissues, within cells
	e	accumulation of salt in xylem parenchyma in roots and shoots
	f	synthesis of organic solutes
	g	retranslocation of salt to roots and recretion by roots
	h	disposal of older plant parts ("salt-filled organs")
	i	recretion by gland-like structures on shoots
		1 by salt-glands
		2 by salt-bladders
C Tolerance		
	a	increasing salt tolerance of tissues, cells, organelles
	b	increase in halo-succulence
		1 increase in leaf-succulence
		2 increase in stem-succulence, reduction of leaves

Salt resistance of plants can be defined in various ways. Some of these control mechanisms are also active in non-halophytes (Tables 1 and 2, Figure 1), but some of them are very specific features, which have evolved in halophytes. Moreover, it is obvious that not only one of these mechanisms is active in different types of halophytes. One set can be active in one group, whereas another set of mechanisms is dominant in another group. This has lead to the classification of halophytes into salt-excluders, salt-includers (often possessing means of salt-recretion) and salt-accumulators (often halosucculents).

It has to be stressed that salt resistance has at least two quite differing aspects: The one is the upper limit of salt that can be tolerated by an individual plant, the other is the existence of a plant species that exerts successful reproduction. Salt resistance of plants varies very much. It varies

- during different growth or development phases
- with ionic constitution of the soil solution
  (e.g. the presence of Ca, K as antagonists of Na)
- with microclimatic conditions (e.g. relative humidity)
- with life form and halophyte type
- with the plant organ affected by salinity
- with the genetic variability of each species forming ecotypic varieties

TABLE 2. Salt resistance of plants (acc. to Richards, 1954; Waisel, 1972; Breckle, 1976; Albert, 1982)

A Ecological Aspect:	
	The ability of plants to survive and to complete their life-cycle under saline conditions
	□ determines survival ability and endurance; criterion for wild species; growth, size, yield, are neglected
B Physiological and Ecophysiological Aspect:	
	The relative ability of a species to grow on saline soils in comparison to its growth on nonsaline, conditions
	□ determines adaptabilities of species more than their ultimate resistance
C Agricultural Aspect:	
	The relative ability of a species to grow and yield on saline soils in comparison to other species
	□ determines yield

Salt tolerance of a plant is not defined by the act of individual genes, by the individual regulation of each of them or by one specific metabolic process, salt tolerance is a whole plant response (Hedenström and Breckle, 1974; Breckle, 1990, 1995; Munns, 1993; Naik and Widholm, 1993; Flowers and Yeo, 1995; Ramani and Apte, 1997), where many processes, such as efficient K-pumping and accumulation, synthesis and transport of compatible solutes, plant signaling systems involved in tissue and in developmental regulation (Winicov and Bastola, 1997) etc., are only some important adaptations.

3.2.2 MULTILEVEL EFFECTS OF NaCl

Salt affects plants in various ways and on different complexicity levels. There are the osmotic effects (Albert, 1982; Sitaramam and Madhavarao, 1997; Pardossi *et al.,* 1998) and the specific ion effects to be distinguished (Neumann, 1997). Both affect in different ways the cytoplasmic structure and metabolic processes. On the level of the individual plant these processes are underlying genetic and hormonal control. Thus formative effects are genetically determined as well as modificatively influenced (e.g. Suarez *et al.,* 1998). On the level of a plant community the ecological success, which is influenced by dry matter production, carbon partitioning, growth and seed set, may alter the competitive ability of a species. Under field conditions, i.e., under competition with other species, and under varying abiotic and biotic factors, a distinct pattern of dominance in a plant association develops. Selection of more resistant ecotypes may lead to an altered composition and in the long run change the community structure.

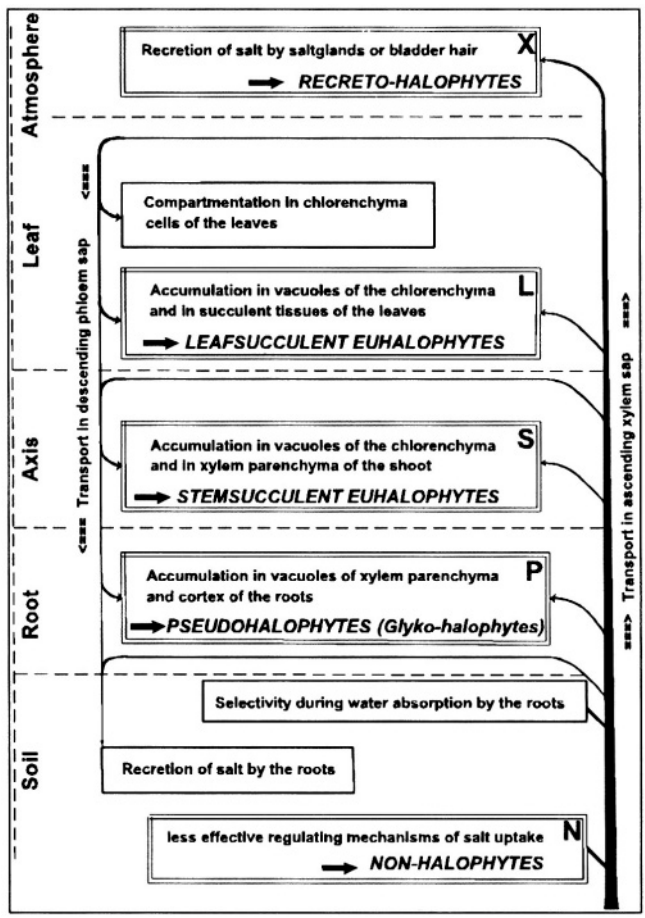
Atmosphere
Recretion of salt by saltglands or bladder hair
X
RECRETO-HALOPHYTES
Leaf
Compartmentation in chlorenchyma cells of the leaves
Accumulation in vacuoles of the chlorenchyma and in succulent tissues of the leaves
L
LEAFSUCCULENT EUHALOPHYTES
Axis
Accumulation in vacuoles of the chlorenchyma and in xylem parenchyma of the shoot
S
STEMSUCCULENT EUHALOPHYTES
Root
Accumulation in vacuoles of xylem parenchyma and cortex of the roots
P
PSEUDOHALOPHYTES (Glyko-halophytes)
Soil
Selectivity during water absorption by the roots
Recretion of salt by the roots
less effective regulating mechanisms of salt uptake
N
NON-HALOPHYTES
Transport in descending phloem sap
Transport in ascending xylem sap

Figure 1. Schematic classification of halophyte types according to strategy of regulation of internal salt concentration (Breckle, 1976)

3.3 Halophyte types

3.3.1 CLASSIFICATION

Halophytes can be grouped to a specific halophyte-type, according to most relevant mechanisms for salt resistance (Figure 1). However, since intensive halophyte ecology research has started (Stocker, 1928; Waisel, 1972), there were long discussions how to classify halophytes and many classification systems had been proposed (Breckle, 1990).

It is most promising to use the ecophysiological approach in defining halophyte types. Thus, as demonstrated in Figure 1, halophyte types can be characterized by the dominance of processes regulating salt transport in plant organs according to accumulation and recretion of salts, thus maintaining a distinct saltbalance.

Most of the halophytic genera can be placed distinctly in one of these groups (Figure 1). Very few exhibit intermediate characters or change from one to another category with age (e.g. *Halimione*).

For halophytes it is characteristic that osmotic adaptation is accomplished by absorbing inorganic ions (expressed as Cl^- in Figure 2), counterbalanced by compatible solutes in the cytoplasm. As a rule the osmotic potential of leaf cell sap differs normally by 0.5 to 1 MPa from that of the soil solution (Figure 2), enabling uptake of water.

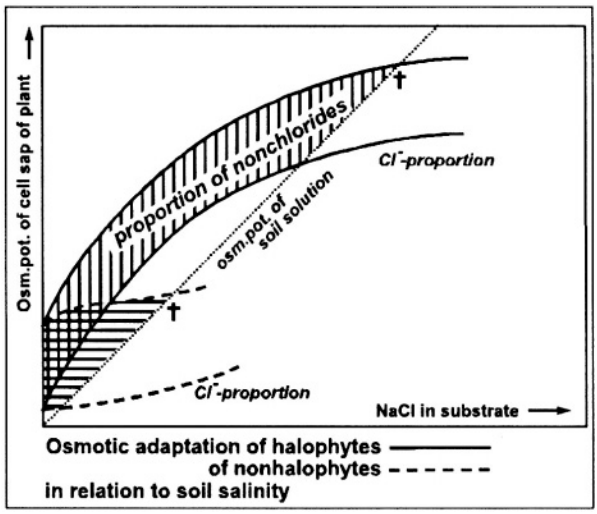

Figure 2. Osmotic adjustment in halophytes and nonhalophytes (□: maximum NaCl concentration, where osmotic adaptation is zero and thus plants start suffering)

3.3.2 GROWTH OF HALOPHYTES

In many halophytes it was shown that growth is stimulated by salt. According to growth response curves Kreeb (1974) has distinguished four plant types, as is shown in

Figure 3. Halophytes were defined those which exhibit maximal relative growth under some salinity in the substrate.

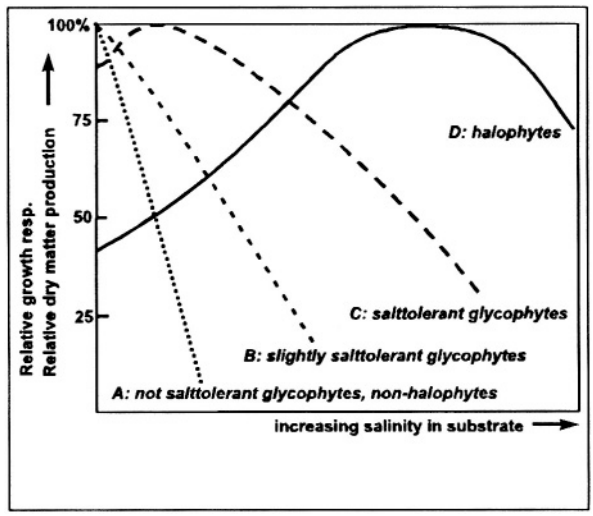

Figure 3. Schematic graph indicating growth of various types of plants under salt-stress (modified from Kreeb, 1974)

However, it has not been taken into account, if growth of the root system and/or the shoot is equally affected. An increased shoot/root ratio with increased salinity was shown by Osmond (1980) for *Atriplex*-species. But Clarke and Hannon (1970) reported a distinct decrease of shoot/root ratio with increasing salinity for a number of Australian saltmarsh plants, Shalhevet *et al.* (1995) for maize and soybean. It should be mentioned that other ecological factors, such as, nitrogen availability can greatly change growth. Moreover, under drought stress salinity enhanced growth in various *Atriplex*-species (Glenn and Brown, 1998), indicating an important role of ion uptake in halophytes.

Roots are in direct contact with the saline soil solution. Salinization results in shorter and thicker roots (Cramer *et al.,* 1991) and it seems again, that not only osmotic effects but also specific ion effects cause an additional depression of growth (Kafkafi and Bernstein, 1996). A change in architecture of the root system under salinity can be deducted from results of Waisel and Breckle (1987). They have shown that the laterals are more affected by NaCl than the taproot. A horizontally spread root system under nonsaline conditions develops to a more vertically oriented root system under salinity. Unequal distribution of salts in the root environment was investigated by Sonneveld and Kreij (1999). Nutrients were readily absorbed also from roots under high salinity, whereas water was preferably absorbed from the root parts with the lowest salinity.

In various chenopods it was shown that growth was stimulated by moderate salinity (Breckle, 1976). The best way to define growth is using ash free dry matter (organic matter) increment, which often in literature is not reported. Plant mineral content in

halophytes may be of such magnitude that changes in organic matter could be obscured.

Since growth in halophytes is enhanced by salinity in contrast to nonhalophytes, this leads to the question whether halophytes need salt obligatorily. As obligatory halophytes only would strive successfully on saline soils the question arises if they can live on nonsaline soils. It has been shown that sodium is an essential micronutrient only in C4- and in CAM-plants (Brownell, 1979 – Chapter 16), but deficiency symptoms are known only under experimental conditions. The same is known for chloride (Epstein, 1980, 1985; Engel *et al,* 1997). There are no indications that any saltmarsh or mangrove species is an obligate halophyte, they all can be grown successfully under garden cultivation, but if they also can complete their whole life-cycle successfully under such conditions it was not proven. The effects of salinity on different growth stages and growth processes of plants also have to be taken into account (Ungar, 1996). Germination and seedling growth is normally more sensitive than growth of established adult plants. Köhl (1997) has shown that ecotypic differentiation of closely related salt marsh and inland taxa of *Armeria maritima* is not very significant in respect to salt tolerance though it is rather obvious for heavy metal resistance. Halotolerance depends largely on the osmotic adjustment of cytoplasm through accumulation of compatible solutes (Wyn-Jones *et al.,* 1977; Popp, 1985; Shomer-Ilan and Waisel, 1986; Solomon *et al.,* 1994; Gzik, 1996; Hare and Cress, 1997). Screening for salt resistance must be based on a good knowledge of the involved traits and on understanding of the internal metabolism in plants with an appropriate content of organic protectants (Waisel 1989).

Salts taken up by halophytes do not directly control plant growth by affecting turgor, photosynthesis or the activity of one or another enzyme. The build-up of salts in old leaves hastens their death. The loss of leaves affects the supply of assimilates or hormones to the growing organs and hereby affects growth (Munns, 1993; Munns *et al.,* 1995). As a conclusion certain forage crops might be cultivated by irrigation with brackish water without any yield reduction for a shorter period but not with seawater (Pasternak *et al.,* 1995). Contamination of soils with sodium should be avoided in any agricultural system. Break-down of physical soil structure by sodium leads inevitably to growth reductions.

3.3.3 ION-RATIOS

Halophytes can be classified into Chloride-Halophytes, Sulfate-Halophytes and Alkali-Halophytes, according to the main ions in cell sap or ash (Walter, 1968). The Alkali-Halophytes are those, where a high proportion of organic acids (e.g., oxalate for example in *Halogeton* with up to 30% of dry matter) are accumulated. It is long known that halophytes are able to take up nutrients from the soil despite of an excessive content of Na^+ and Cl^-. Most halophytes are discriminating Na^+ against K^+ and only few species are sodiophilic. To demonstrate the characteristics in K^+/Na^+ - discrimination it is necessary to have the relevant soil samples from the rhizosphere. Various halophytes from Iran and Afghanistan were analyzed and K^+/Na^+ -ratio in the

substrate and in the plants is plotted (Figure 4). The oblique lines (f) give an idea of the accumulation factor for sodium in comparison to potassium. It is easily visible that most species under a wide range of given cation ratios in the soil favour potassium uptake. Only the Chenopodiaceae *Salicornia europaea* and *Suaeda maritima* can be termed sodiophilic. In contrast the grass *Puccinellia distans* very selectively accumulates potassium by a factor of 100 even in very saline soils.

Under controlled conditions with hydroponics or sand-culture it is possible to check the ion discrimination by different halophyte types in an even better way and this leads to characteristic indicator lines according to the given ion-ratio (Figure 5). This demonstrates again that selectivity varies according to ion ratio in the nutrient solution. Under equimolar K^+/Na^+ culture solution only the stemsucculent *Allenrolfea* is sodiophilic, whereas the leafsucculent *Sarcobatus* and even more the pseudohalophyte *Ceratoides* are potassiophilic. However, under a high supply of potassium even *Ceratoides* becomes sodiophilic, and under a very high relative supply of sodium even *Allenrolfea* becomes "potassiophilic", when comparing only with the 1:1-line.

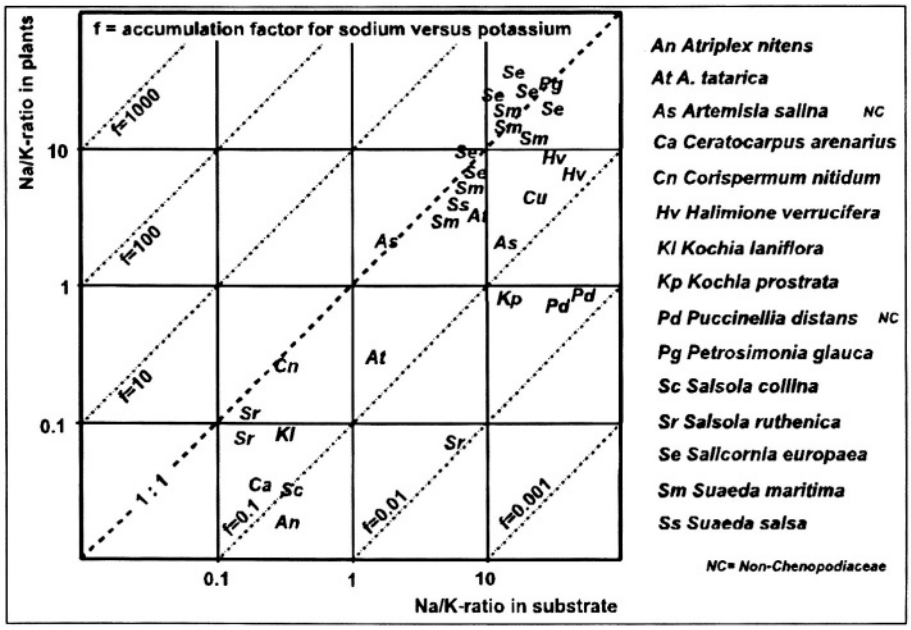

Figure 4. Ion ratio of Na/K in soil and plants indicating potassiophily (Mirazai and Breckle, 1978)

Several grades of K^+/Na^+ selectivity and sodium exclusion were demonstrated for halophytic and nonhalophytic members of the Chenopodiaceae (Reimann, 1992; Reimann and Breckle, 1993). Thus the various members of the Chenopodiaceae can not be put in one group of physiotypes. The two halophytes *Suaeda maritima* and *Atriplex prostrata* exhibited a pronounced Na^+ accumulation in the shoots.

High levels of NaCl accumulation are not necessarily a prerequisite of high salt resistance in halophytes of the salt accumulation type. Glenn *et al.* (1992) investigated low-sodium and high-sodium ecotypes of *Atriplex canescens* over a range of salinities up to 720 mol m^{-3} NaCl. Clear differences in Na^+ and K^+-accumulation and Na^+/K^+ ratios were not paralleled by a difference in salt resistance. This means, salt resistance is more than tolerance against high internal salt concentrations. Anyhow, the capacity of plants to maintain a low cytosolic Na^+/K^+ ratio is likely to be one of the key determinants of plant salt tolerance (Maathuis and Amtmann, 1999; Chapter 8). Under natural conditions the Na-levels vary very much, but also the levels of other ions. There are many papers on the chemistry of halophytes and their internal ion composition (Albeit, 1982), as well as on the normally taxon specific accumulation of compatible solutes (Popp, 1985). Such results indicate an ion homeostasis in halophytes under NaCl stress, which partly is explained by the relevant ion transport across the cell membranes (see Niu *et al.,* 1995) of the various tissues functioning as storage cells by maintaining their internal steady state.

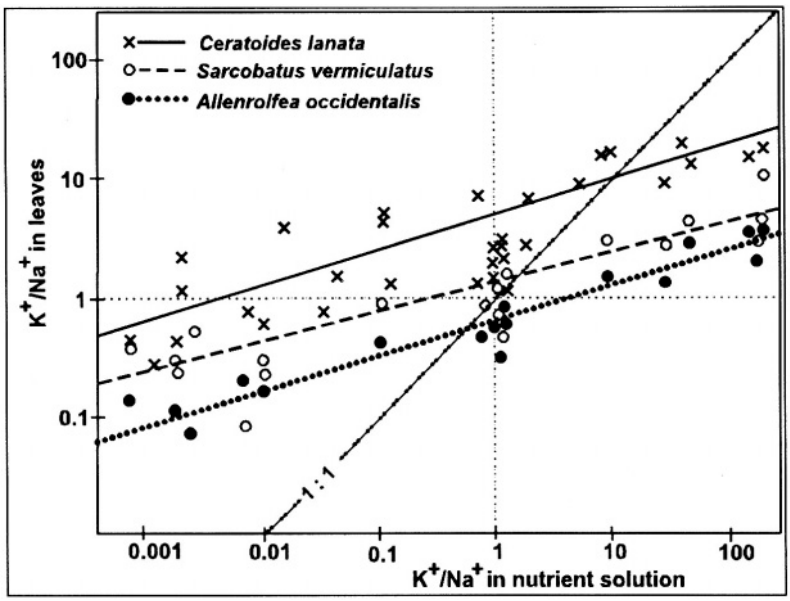

Figure 5. Ion ratios (K/Na) in nutrient solution and leaves in three North American halophytic species, differing in their potassiophily (Breckle, 1976)

Calcium has an ameliorating effect upon the tolerance of higher plants to salinity (Munns *et al.,* 1983; Epstein, 1998; Chapter 10) and the availability of Ca plays a major role in counteracting salinity stress (LaHaye and Epstein, 1969), but not in all plant organs (Caines and Shennan, 1999) and not in all growth stages (Wilson *et al.* 2000). Carvajal *et al.* (2000) could relate the ameliorative effect of Ca^{2+} to water-channel function in cell membranes of roots.

In some parts of the world salinity is not caused only by chloride, but in temperate and cold arid regions it may be by sulfate or carbonate accumulation (Curtin *et al.,* 1993). In other areas the accumulation of soluble boron compounds concomitantly with chlorides can cause high toxicity problems. Chloride and borate behave antagonistic in uptake by some halophytes (Holloway and Alston, 1992), however, Grieve and Poss (2000) found a strong interaction of external B and salinity to limit growth and yield of wheat.

3.3.4 SUCCULENT EUHALOPHYTES

Succulent halophytes are either leafless and stem-succulent or have fleshy and succulent leaves. In both cases this kind of succulence has two components, the basic one is a genetically controlled succulence, whereas the second is a modificative variable and can be induced by salts to a considerable degree. These types of halo-succulence have to be distinguished from xero-succulence.

3.3.4.1 Leaf-succulent- Eu-Halophytes

The typical leaf-succulent halophytes are characterized by almost cylindrical or globular leaves (examples are: *Triglochin maritima, Plantago maritima,* and many species of *Salsola, Suaeda, Nitraria* etc.). The salt-content of those leaves can reach up to 60% of dry matter (Eshel, 1985), the concentration of salt in cell sap about 1500 mol m^{-3} NaCl (Waisel, 1972).

The degree of succulence varies with external salinity, NaCl being more effective than sulphate-salinity. In some halophytes only some tissues in the leaves become succulent, in others all tissues grow larger and accumulate more cellsap. A higher tissue water content goes normally parallel with a lower tissue elasticity and a greater hydraulic conductance (Youngman and Heckathorn, 1992).

Some halophytes show a great increase in succulence already at low salinities. Thus, the view, that increased halo-succulence is a means for regulating ionic content of the tissues (as some kind of dilution) may be inappropriate (Storey and Wyn-Jones, 1979). It could be speculated that it might be a "cheap" possibility of increasing leaf-area for photosynthesis by low energy costs (Y. Waisel, personal comm.).

There are leaf succulent halophytes which are annuals, e.g., some *Suaeda*-species, *Halopeplis, Halimocnemis, Gamanthus* etc.. Tremblin and Ferard (1994) have shown, that *Halopeplis* has an extraordinarily high growth optimum at 200-300 mM NaCl in the medium. Other leaf-succulents are herbal perennials (such as, e.g., *Plantago, Aster, Suaeda*), and others are shrubs (e.g., some members of the genera *Salsola*, *Suaeda*, *Nitraria, Kochia/Maireana*). In some others the succulence of the fruit or parts of the fruit became very pronounced (*Gamanthus*, or in many Mesembryanthemaceae). Regarding the adaptations of the photosynthetic pathway, which have evolved, it is obvious that succulence has altered the anatomical structure dramatically, as can be seen in the various types, that are exhibited by *Salsola* and *Suaeda* (Shomer-Ilan *et al.,* 1981).

3.3.4.2 Stem-succulent Eu-Halophytes

As in leaf-halosucculents it is thought that also in stem-succulent halophytes the high salt-concentration in the plant body is mainly restricted to the large vacuoles of storage tissues cells. It was often said, that this is part of the mechanism that is responsible for diluting the salt-concentration of the salt-affected cells.

There are different lifeforms known in stem-succulent halophytes, annuals such as, e.g., *Ofaiston, Salicornia,* but also herbal perennials, (e.g., *Arthrocnemum, Anabasis,* etc.) and halfshrubs and shrubs, with woody base (e.g., *Halocnemum, Halostachys, Aellenia, Haloxylon, Kalidium,* etc.).

3.3.5 SALT-RECRETING HALOPHYTES (CRINO-HALOPHYTES)

Many halophytes exhibit a rather rapid turnover of their leaves. The rosette leaves in *Limonium vulgare* are replaced during the vegetation period 2 or 3 times, the leaves of *Aster tripolium* rather soon become yellow and new leaves replace them. This replacement is a mechanism of removal of large quantities of salt. Old leaves with high salt content are steadily replaced by younger leaves in many *Juncus* species. This is certainly one adaptation mechanism that enables the plant to get rid of excessive salts by shedding plant organs.

But even more important in some halophytes is the existance of specific cell structures which can recrete (recretion in the sense of Frey-Wissling, 1935: elimination of substances not metabollically changed) inorganic ions, especially NaCl. This is done by salt-glands, which have evolved several times in the angiosperms, and by bladder hairs. Salt glands eliminate salt to outside, bladder hairs accumulate salts in their huge vacuole, in both cases the salts are physiologically isolated from active tissues.

3.3.5.1 Halophytes with salt glands

Salt glands were first described by Volkens (1884) in *Limonium* and by Marloth (1887) in Tamaricaceae.

Salt glands are found in various halophytic plant genera, the main examples are listed in Table 3, exhibiting striking differences in anatomical structure. The most complex glands are the salt glands of the Plumbaginaceae (Wiehe and Breckle, 1989). The density of the salt glands is between 600 and 5000 per cm^2 leaf area.

The processes of salt recretion by glands were extensively studied only in a few species (see discussion in Waisel, 1972; Breckle, 1976), and it was shown that active transport plays the major role. The selectivity against ions differs in the various species according to their natural occurence. The halophytes *Limonium gmelinii* and *L. ramos-sissimum* are very potassiophilic, as can be seen by the strong change in ion pattern (Figure 6, left side) between nutrient solution and leaf cell sap. Again, there is a major change in ion composition between leaf cell sap and the recreted fluid. The ion pattern changes in such a way that the cytoplasm of the leaf cells is kept relatively low in sodium, whereas the gland fluid is rich in sodium (Figure 6, right side). Such a behaviour is not recognizable in *Limonium sinuatum,* a plant which comes from

slightly saline stands. In that species selectivity in both cases of transport is low (Figure 6). It was also shown that the activity of the salt glands of the halophilic *Limonium* species (Wiehe, 1986) and *Aeluropus* have a threshold value and start to recrete NaCl only after a distinct salinity level in the leaf is reached (Pollak and Waisel, 1979).

In *Aegialitis annulata* about 26% of the internal salt content of young leaves (old leaves: 2%) is removed within 12 hours by the gland activity, when grown on 50 mol m^{-3} NaCl, but 38% (old leaves: 29%), when grown in 500 mol m^{-3} NaCl (Popp *et al.,* 1993). This is not so for *Avicennia,* where salt-filtration by the roots is by far the most important salt-rejecting mechanism (Waisel *et al.,* 1986).

TABLE 3. Halophytic plant genera possessing active salt glands

Plant family and genus		number of cells per salt gland
Convolvulaceae	*Cressa*	??
	Ipomaea	??
Frankeniaceae	*Frankenia*	??
Plumbaginaceae	*Armeria*	16
	Limoniastrum	16
	Limonium	16 or 20
	Plumbago	16
Poaceae	*Aeluropus*	2
	Chloris	3
	Spartina	2
	And many other grass genera	
Primulaceae	*Glaux*	??
Tamaricaceae	*Reaumuria*	??
	Tamarix	8
and in mangroves (Popp, 1985):		
Acanthaceae	*Acanthus*	8
Avicenniaceae	*Avicennia*	(5)-8-(9)
Myrsinaceae	*Aegiceras*	??
Plumbaginaceae	*Aegialitis*	40

Marcum *et al.* (1998) have checked 57 accessions from *5* species of *Zoysia* (grasses with two-cellular glands) for recretion of NaCl during 400 mol m^{-3} NaCl culture. Relative salinity tolerance was negatively correlated with leaf sap NaCl and positively correlated with leaf salt gland recretion rate and leaf gland density. Gland structure and function were investigated by Liphschitz and Waisel (1982).

The salt glands of *Tamarix* produce an alkaline recretum (Waisel, 1992). It is suspected, that this could promote a triplet of purposes: a) remove excess mineral ions out of the live parts of the leaves; b) recrete hygroscopic solutes, thus, providing the plants with a moist cover and reducing the time during which transpiration occurs; c) award plants with an enriched environment of CO_2, as a type of carbon enrichment system which might improve photosynthesis during early morning hours. Such an enriched environment reduces respiration and improves salt resistance of those plants.

3.3.5.2 Halophytes with bladder hairs

Not only glands but also bladder hairs can remove salts from essential and salt-sensitive metabolic sites in the leaf mesophyll and from the embryonic tissues close to the shoot-tip. Salt accumulating bladders are well known in several genera of the Chenopodiaceae, typical in most *Atriplex*-species (Schirmer and Breckle, 1982; Breckle, 1992). They are composed normally of one or more small stalk cells, functioning as gland cells and a huge bladder cell, functioning as a reservoir (Black, 1954, Berger-Landefeldt, 1959). The cell wall of the stalk cells seems to be largely cutinized preventing

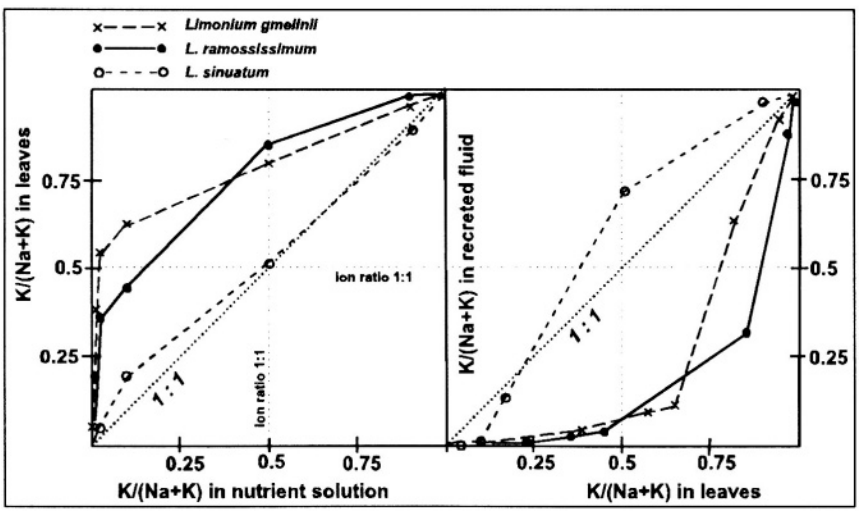

Figure 6. Ion ratios (K/Na+K) in three *Limonium* species differing in salt tolerance. Left side: Correlation between nutrient solution and leaves; right: Correlation between leaves and recreted fluid from salt glands (Wiehe, 1986)

apoplastic backflow of salt from the bladder to the mesophyll (Freitas and Breckle 1993).

Accumulation of sodium and chloride in the bladders was detected in many species of *Atriplex,* suggesting their role in the ionic balance of these plants (Freitas and Breckle 1994). According to Osmond (1979), more than 50% of chloride content in *Atriplex* leaves is recreted to the bladders. The percentage of sodium and chloride in bladders in relation to leaves in *Atriplex rosea* was rather similar in different salt treatments (Freitas and Breckle, 1994), no increment was verified in the highest treatments. The contribution of bladder hairs to the regulation of sodium and chloride is, to some extent, determined by the salt concentration of the leaves. Even excessive nitrate can be recreted to bladders. In young leaves of seedlings the ionic balance and regulation ability is not well developed. Thus, available ions are accumulating in the leaves, and bladder hairs become an important mechanism for ionic balance for the developing leaves (Freitas and Breckle, 1994).

Similar bladders as in *Atriplex* are reported for *Chenopodium, Salsola, Halimione* etc. The ecological significance of bladder bearing species is still under dispute, but if one takes into account, that vast areas of semideserts are covered by low shrubby vegetation of *Atriplex* and other chenopods, it can be suggested, that this is likely to be one of the successful mechanisms for adaptations to salinity.

Conversely, the huge epidermal cells of the Mesembryanthemaceae (Aizoaceae) do not appear to function as salt deposition structures, and function probably as water storage tissues (see Chapter 16).

3.3.6 PSEUDOHALOPHTYES AND NON-HALOPHYTES

Saline vegetation types often are composed of several species, where some of these species are not real halophytes. They occur only accidentally in such plant-communities of oligohaline marshes, but have their optimal growth and performance in nonsaline vegetation. These plants might have a slightly higher salt tolerance (Howard and Mendelssohn, 1999). Normally such plants lack specific anatomical features, but may become slightly succulent under salinity as a modificative character (*Plantago major*). Non-halophytes (Glycophytes) also can become somewhat succulent under salt stress, as was demonstrated with many cultivated species (Stroganov, 1964). The strong formative effects on leaf structure of saline conditions were shown by Waisel (1972). Not only does salinity increase the cell size, but also it changes the density of stomates, changes the ratio of palisade and spongy parenchyma etc.

The number of species which exhibit special salt tolerant ecotypes is rather large. Ellenberg *et al.* (1991) have characterized them by an indicator value for halophytic performance (see Table 4).

3.3.7 HALOPHILIC GRASSES

There are several grasses which are highly salt-tolerant (Table 4); for C4-grasses see Chapter 16, but euhalophytic halo-succulents, are not represented among the grasses.

Although osmotic adjustment by storage of organic solutes is regarded more costly energetically than storage of Na^+ and Cl^- (Yeo, 1983), in salt-excluding species the more salt-resistant ecotypes are those with a greater restriction of Na^+-accumulation in the shoots. Comparing two populations of *Hordeum jubatum* from a saline and one of a nonsaline site, Wang *et al.* (1992) found lower Na^+-concentrations in the shoots of the plants originating from the saline habitats, when they were treated with 148 mol m^{-3} Na^+ in hydroponic solutions. This confirms findings by Rozema (1976) on ecotypes of *Juncus,* it seems to be rather characteristic for graminoids, which, as a rule, are very efficient salt-excluders (Albert, 1982). In the salt-recreting grass *Spartina alterniflora* a dwarf ecotype was recently found (Daehler *et al.,* 1999).

They use 10 numerals for characterizing ecological behaviour of a plant species in relation to salinity. On the other hand, the occurence of those species can be used to

characterize vegetation types without chemical analyses, just by determining and calculating the various indicator values from the Ellenberg-lists.

TABLE 4. Indicator-values for halophytic plants from the Flora of Central Europe, indicating the ecological behaviour against salinity (Ellenberg *et al.*, 1991)

0 :	not salttolerant, never in brackish soils
1 :	salttolerant species, which can withstand some salinity, but most frequently occuring in nonsaline soils ("pseudo-halophytes") [0-0.1%Cl^-]
2 :	similar as 1, but more often in slightly brackish soils [oligohaline, 0.05-0.3%Cl^-]
3 :	species indicating salinity, may, however, also grow in soils with low salinity ("facultative halophyte" in ecological sense) [ß-mesohaline, 0.3-0.5% Cl^-]
4 :	similar as 3 [a/ß-mesohaline, 0.5-0.7%Cl^-]
5 :	similar as 3, normally only in saline soils [a-mesohaline, 0.7-0.9%Cl^-]
6 :	typical halophytes, indicating salinity, rare in nonsaline soils [a-meso-/polyhaline, 0.9-1.2%Cl^-]
7 :	similar as 6, but very salttolerant, never in non-saline soils ("obligatory halophytes" in ecological terms) [polyhaline, 1.2-1.6%Cl^-]
8 :	typical halophytes, indicating high salinity, very salttolerant [euhaline, 1.6-2.3%Cl^-]
9 :	extrem halophytes, in soils with very high, during dry periods extremely high salinity ("obligatory halophytes" in ecophysiological terms) [euhaline/hypersaline, >2.3%Cl^-]
m :	average of salinity-indicator-values (1-9, without 0)

Indicator-value:	1	2	3	4	5	6	7	8	9	m
Number of species										
Dicotyledonae										
Amaranthaceae	3									1.0
Apiaceae	7		2	1						1.7
Asteraceae	12	2	2		2	1		1		2.0
Brassicaceae		2	2	2				1		3.7
Caryophyllaceae		2		1	1			1	1	5.0
Chenopodiaceae	1		1		1	1	4	3	2	6.5
Euphorbiaceae	1									1.0
Fabaceae	8	4		1						1.5
Gentianaceae	2				1					2.3
Lamiaceae	3									1.0
Lythraceae	1	1								1.5
Malvaceae	2									1.0
Onagraceae	3									1.0
Plantaginaceae	1	1		1			1			3.5
Plumbaginaceae						1		1		7.0
Polygonaceae	1	2	1							2.0
Primulaceae				1			1			5.5
Ranunculaceae	2	1								1.3
Rosaceae	1									1.0
Scrophulariaceae	3			1						1.7
Solanaceae	1									1.0
Violaceae	1									1.0
Monocotyledonae										
Cyperaceae	8	4	1		3	1				2.4
Juncaceae	3	1	1	1		1	1			3.1
Juncaginaceae			1					1		5.5
Poaceae	9	5	2	1	2	4	3	2		3.6
Potamogetonaceae	4				1			2	2	5.4
Typhaceae	1									1.0

3.4 Natural saline ecosystems

3.4.1 SALINE COASTAL ECOSYSTEMS

There are many descriptive accounts on salt marsh vegetation (e.g. Adam, 1990). The main approaches are using structural and physiognomic attributes and/or floristic data for circumscription of plant communities. The initial similarity in appearancof salt marshes allows only a small number of categories, hence salt marshes are also treated as azonal vegetation types. On the basis of their dominant growth form it is possible to recognize three categories:

- Herb communities
- Graminoid communities (with grasses, sedges, and rushes)
- Dwarf shrub communities

At most sites all three types of communities co-exist. However, arctic and boreal marshes are predominantly covered by graminoid marshes, while dwarf shrub marshes are extensively developed along arid and semi-arid tropical and subtropical coasts.

The lifeforms of halophytic species in salt marshes are predominantly Hemicryptophytes (acc. to Waisel, 1972, e.g., in Europe 40%; in Israel 35%), Therophytes (30%; 19%), Chamaephytes (10%; 29%); Phanerophytes (0%; 17%) and Cryptophytes (10%; 0%). In most salt marshes all over the world the hemicryptophytes are the dominant lifeform, only in the tropics (mangrove) the phanerophytes dominate. The question, why there are no salt tolerant bigger shrubs and trees in the temperate climatic zones is still an open question (Tomlinson, 1986) and selection of trees for high salinity tolerance is a big need (Sun and Dickinson, 1995).

Coastal salt marshes and mangroves are found between the high tide and the near-shore sublittoral zones, not only along coasts, but also in estuaries of continents. They often flourish in regions where much silt is carried to the coastal regions by rivers or where geological processes favor erosion and suspension of silt. Salt marshes have a high rate of primary productivity. Processes in salt marshes are governed by the interactions of abiotic (physical, chemical and geological) and biotic (herbivory, parasites, decomposition) factors (Vernberg, 1993). Above-ground vegetation and seed bank composition of zonal communities along salinity gradients is usually not highly correlated. Since seeds of annual salt marsh species occur in all zones, the levels of salt stress may be the main factor determining which species is found in the above-ground vegetation (Egan and Ungar, 2000). Material cycling, biogeochemical and nutrient cycling as well as overall productivity for ecosystem functions and interactions with adjacent ecosystems are major processes and are suspect to typical long-term changes, since salt marshes are typical ecotones.

3.4.1.1 Salt marshes in temperate regions

By using the dominant species concept a number of salt marsh communities can be distinguished. In addition, however, the full floristic composition gives a better picture

in species-rich communities on the recurrent group of species. Normally salt marshes are poor in species and individual species in most genera have a wide ecological amplitude, except e.g. in *Limonium.*

Along the zonation with vegetation belts parallel to the sea shore, with increasing elevation and decreasing number of tidal inundations these vegetation belts exhibit a strong ecological gradient. Salinity decreases with elevation. The salinity limits between the vegetation belts predominantly determine the occurence of the phytosociological vegetation units (Figure 7) by competition between species as members of the units.

Salinity normally is negatively correlated with species richness (Garcia *et al.,* 1993). A comparison of zonation pattern between larger areas is difficult because the tidal influence (number and duration of submergences) may be different as well as the floristic pattern, the geographical and climatical features and substrate conditions.

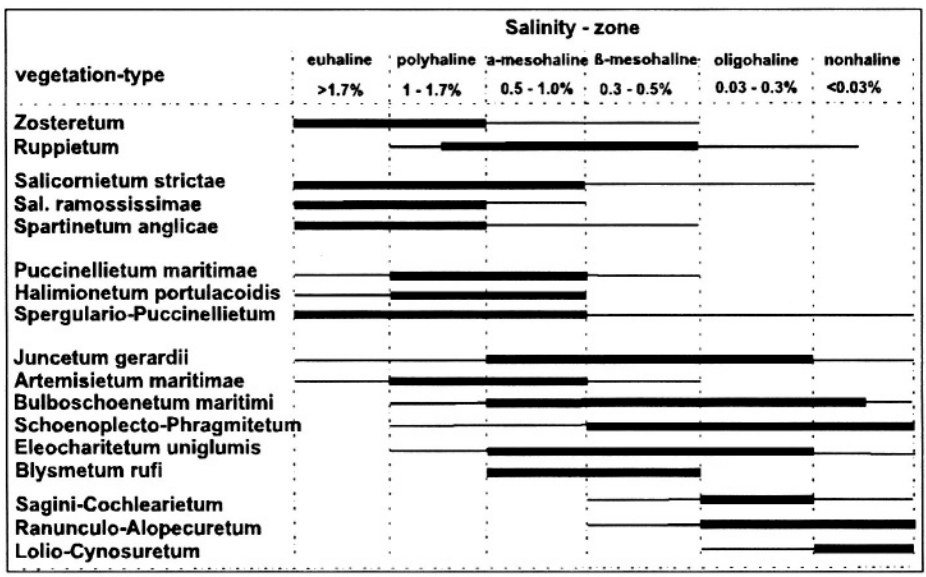

Figure 7. Optimal ranges and amplitudes in salinity of main vegetation types along Southern Scandinavian coasts (Dierssen *et al.,* 1991; Dierssen, 1996)

Substrate conditions according to sedimentation may be altered by trapping of sediments. This may lead to a long term succession with longtime stable vegetation limits, but by sudden episodic events, such as storms or strong floods the present vegetation mosaic might undergo rapid changes in species composition.

With increasing elevation, species diversity and diversity of plant communities tends to increase. The extreme upper marsh, the ecotone to the non saline plant communities, is the transition to other habitats. It is a region of high heterogeneity, strong

environmental gradients and considerable temporal variability. This narrow zone normally supports a wide range of communities and a rich flora.

3.4.1.2 Mangrove forests

Mangroves (see Chapter 6) occupy the tropical and subtropical habitat equivalents of the salt marshes of the temperate regions. In arid regions the mangrove is separated from inland vegetation by an open extremely saline flat, often bare of vegetation, whereas in tropical humid areas the salinity gradually decreases (Walter and Breckle, 1986, 1991).

3.4.2 SALINE INLAND ECOSYSTEMS

3.4.2.1 Geogenic saline vegetation in humid climates

In humid regions inland salines are sparse. They exist only on geogenic features, where salt-springs come to the surface. Leaching by rain leads to a steady reduction of salinity unless salt is replaced from geological sources. Those inland salines are normally rather small in area, but nevertheless have a rich flora in Central Europe (Wendelberger, 1950). Soil chemistry might differ from one place to another in contrast to coastal marshes, where the similarity in ion chemistry is governed by the overall influence of sea-water.

3.4.2.2 Salt deserts in arid climates

In deserts xerohalophytes are often dominant plant species as a result of coping with the accumulation of salt in soil during long times. In many deserts the mosaic of ecotopes corresponds to a topo-sequence from mountains to accumulation basins. Along these oblique peneplains the particle size in the soil decreases, from rocks, gravel, sand to silt and clay material, giving rise to different desert types, and according to the relevant abiotic transporting means water and wind, sand or loess deserts develop. In the lowest parts the finest particles especially clay and soluble salts accumulate, forming salt lakes with salt deserts.

Within the various desert types saline soils are unevenly present, since geochemic transportation of soluble salts normally results in accumulation in erosion basins. The ecogram of dominant chenopod-halophytes in Northeastern Iran and in the West- and North-Afghanistan (Figure 8), where a highly diverse halophytic flora has evolved, exhibits members in each niche (Breckle, 1982).

The sequence of species along the salt gradient in a rich halophytic area, as it is in the Central Asian deserts, reveals a typical sequence of the dominating halophyte types (Figure 9). Along the salt gradient (Breckle, 1986), which can be derived from salinity measurements in a mosaic vegetation, too, it is obvious, that the stem-succulents (S) and then the leaf-succulents (L) play the major role close to the saline lakes or basins. The recreting halophytes (X) dominate in the middle part of the transect. This part of the transect is often also characterized by less water availability and often here a much higher proportion of C4-plants occur. This is also the case on the less saline side, where then pseudohalophytes (P) and finally on almost saltfree substrates the

nonhalophytes (N) predominate and other ecological factors, such as, e.g., water-availability and -supply, nitrogen-source etc. are governing the vegetation mosaic.

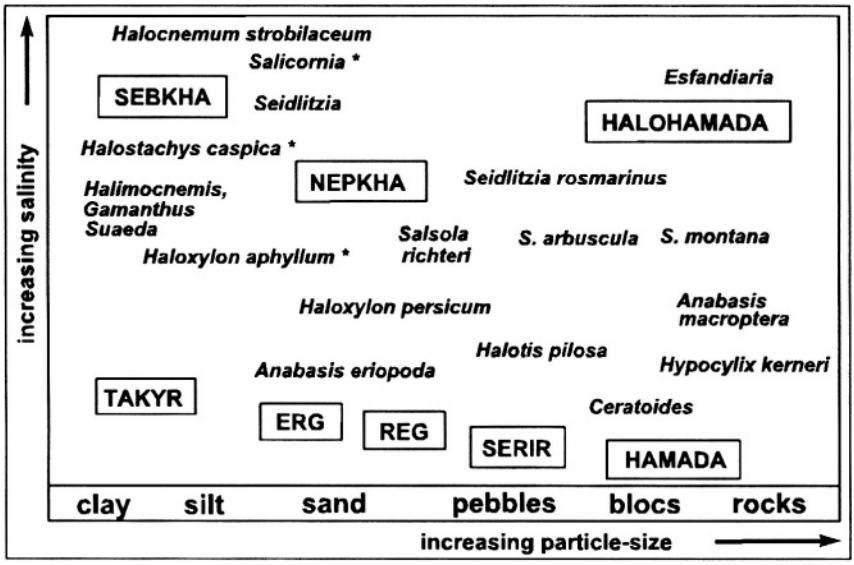

Figure 8. Ecogram of Chenopodiaceae species and correlation to various desert types (mainly for Northeastern Iran and North-Afghanistan). [* = with additional water supply] (Breckle, 1982).
Hamada (rock desert), Serir (pebble desert), Reg (sand and stone pavement desert), Erg (Sand dune desert), Takyr (clay plains) are geomorphological desert types according to substrate particle size; Sebkha (salt desert, salt pans), Nepkha (small, mostly salty sand dunes) and Halohamada (salty bloc desert) are geomorphological desert types under influence of salinity)

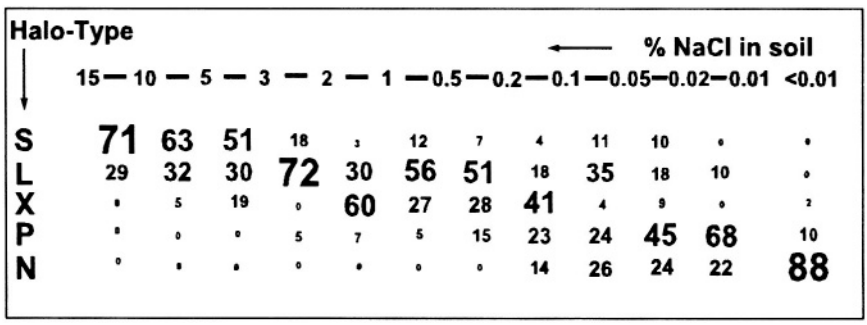

Figure 9: Abundance of halophyte types (% of total species) in halo-catenas in Iran along the salinity gradient (soil salinity, % of dry matter; explanation for S-L-X-P-N, see Figure 1) (Breckle, 1986)

An almost similar sequence of halophyte-types can be derived from the vegetation belts around Great Salt Lake in Utah (Kearney *et al.,* 1914). The ecogram (Figure 10) reveals the similar sequence of S-L-X-P-N halophytes along the salt gradient.

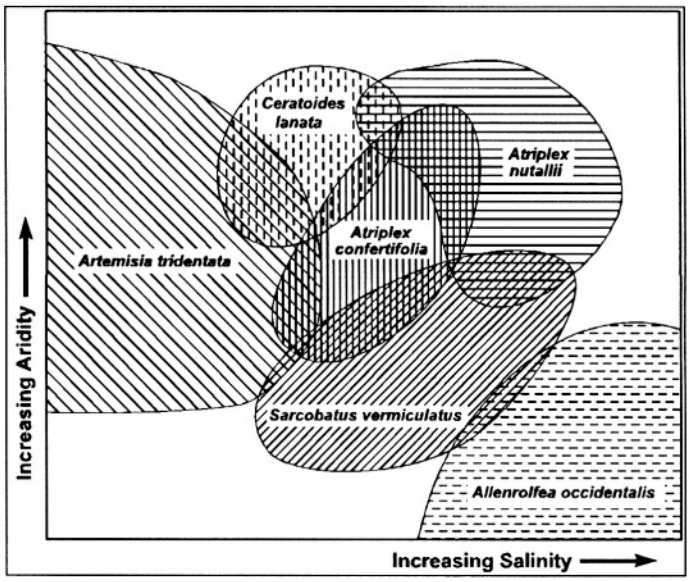

Figure 10. Ecogram showing range of dominant species derived from transects of the Great Salt Lake salt desert according to salinity and aridity (water availability) (Breckle, 1976)

Halophytes often change their substrate themselves by their accumulation of salts and absorption of salts from the soil. This causes on the long run a typical heterogenic salt pattern, with a decreased salinity under the shrubs (Figure 11). The litter, rich in salt, is blown away from the shrubs. In other halophytic communities, however, it could be demonstrated, that saltrich litter is accumulating under the shrubs, such as, e.g., under *Anabasis articulata* in the sanddune ecosystems of the Negev-desert at Nizzana (Veste and Breckle, 1995). Interrelations of plants and soil thus can be very different, according to prevailing factors.

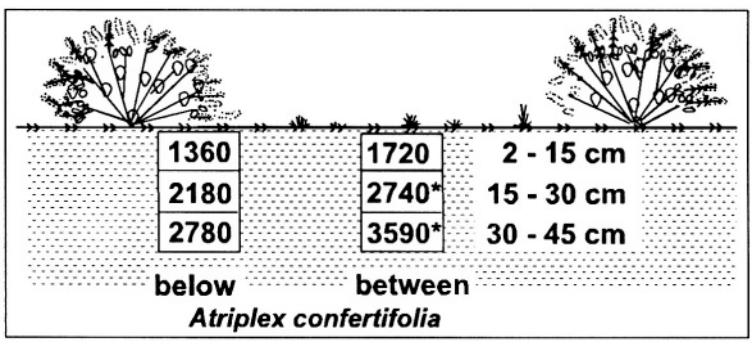

Figure 11. Mosaic of salt concentration in soil shown by significantly different Cl⁻-values in ppm per dry matter between and below halophytic shrubs of *Atriplex confertifolia* (Curlew Valley, Northern Utah, Breckle, 1976).[* : significantly higher values at the 1% level, n = 10]

3.5 Conclusions and Outlook

Adaptive responses among various species show that salt tolerant plants have evolved specialized complex mechanisms, which allow adaptation to saline stress conditions. On the level of tissues, such unique structures as, e.g. salt glands, exist in some plant taxa. Cellular based mechanisms appear to be common in many genotypes and are a prerequisite for salt tolerance, especially the regulation of osmotic adjustment by uptake of inorganic ions (Chapter 8) and/or by synthesis of compatible solutes (Chapter 9). The accumulation and intracellular compartmentation of ions is mainly the result of active transport mechanisms across the plasma membrane and the tonoplast (Chapters 18, 19). Thus all complexity levels have to be taken into account, when considering salinity effects on plants or even ecosystems.

In the future it may turn out that many genes are involved in the complex salt tolerance syndrome (Chapters 21 and 22).

It might be important to find ways, e.g., by quantitative modelling, to extrapolate from one to the next system of complexity. The uppermost level of complexicity: the saline ecosystems, salt marshes and mangroves, need special attention, since they are often sensitive biological areas. The intertidal ecosystems are often very narrow and fragile strips, in many countries already almost totally destroyed but with a very high ecological and potential economical importance.

Ecology of halophytes is still a challenging subject. In spite of research on halophytes for more than 100 years even some basic questions are still unanswered, but will be important, e.g., for breeding halotolerant crops from used crop varieties or by breeding new crops from natural halophyte species. Ion effects, nutrient conditions, osmotic effects, growth and carbon partitioning, intracellular compartmentation, cell wall adjustment and many other interrelated processes on the autecological level have to be checked further in the future. Ecotypes and biogeography, germination and establishment, competition and nutrient availability under high salinity and alkalinity are subjects on the ecosystems level which have to be investigated further.

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